INHERITANCE STUDIES IN PISUM. III. THE INHERITANCE OF HEIGHT IN PEAS*

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As regards height, varieties of peas were classified by Mendel ('66) as either tall or dwarf. When these two types were crossed, the F_1 generation was either as tall or taller than the tall parent. The F_2 generation consisted of approximately 3 tall : 1 dwarf (actual proportions 787 tall : 277 dwarf, or 2.84 : 1). All of the dwarf plants and approximately one third of the tall (28 out of 100) bred true in F_3, while the remaining 72 F_2 talls gave both talls and dwarfs in the ratio of 3 : 1. These results were interpreted as demonstrating a one-factor difference between tall and dwarf varieties of peas.

However, Bateson ('05), Keeble and Pellew ('10), Lock ('05), and others found the inheritance of height in certain cases to be more complex than indicated by Mendel. A class more or less intermediate in height between dwarfs such as Nott's Excelsior and Little Marvel and such talls as Scotch Beauty, Champion of England, and Späte Gold was recognized, to which the name half-dwarf was applied. Such varieties as First of All, Velocity, and Express are excellent examples of this class. Bateson ('05) says half-dwarfs are easily distinguished from talls, and lays particular emphasis on the zigzag growth of the stem as a marked characteristic of this group. If all varieties ranging in height from 3.5 to 4 or 4.5 feet are to be regarded as half-dwarfs, the above statement regarding zigzag growth, in the writer's experience, is only true of one group of half-dwarfs and these have short internodes, as noted later. Evidently Bateson's half-dwarfs are

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all of this type, but those of Keeble and Pellew ('10) and others belong to at least two types.

Crosses between talls and half-dwarfs gave all tall in F_1 and approximately 3 talls : 1 half-dwarf in F_2 in some cases (Tschermak, '02), while in other cases talls, half-dwarfs, and true dwarfs have appeared in F_2 (Bateson, '05, '09, p. 19). Half-dwarfs with long internodes crossed with half-dwarfs with short internodes gave talls with long internodes in F_1 and approximately 9 talls : 3 half-dwarfs (short internodes) : 3 half-dwarfs (long internodes) : 1 dwarf in F_2. The results actually obtained by Keeble and Pellew ('10) were 114 : 33 : 32 : 13—expected 108 : 36 : 36 : 12.

Notes taken by the writer for several years on the height, internode length, and internode number (per plant) of over 200 varieties of peas, grown under similar soil and climatic conditions, indicate a still greater complexity as regards the inheritance and classification of height in varieties of this genus.

For example, tall varieties (over 4.5 feet) may be divided into at least three distinct groups. One type of tall pea has 40 to 60 long internodes (Scotch Beauty, Späte Gold). Another type has 20 to 40 long internodes (Mammut, Goldkönig, White-Eyed Marrowfat). The internodes of each of these types average twice or more the length of the short internodes of the dwarfs. The third type of tall pea varieties is illustrated by Haage and Schmidt's "Graue Reisen Schnabel" which has 21 to 30 very long internodes. Variation in height and internode number among plants of the same true breeding variety is due largely to differences in environment. The absence of the factor for normal stem ($\underset{\smile}{Fa}$), causing fasciation, also brings about a shortening of the internodes. Other types of talls doubtless exist, but the writer's studies have not been detailed enough as yet to recognize them.

Crosses between the three types of talls, so far as they have been made, give in F_1 and F_2 all talls, but talls of different types. Large number of internodes is usually dominant over the low-number types. Sufficient data, as yet, are not available to determine the relation of these types in terms of factorial differences. Each type of tall undoubtedly represents a separate and distinct mutation.

As in the case of the tall-growing varieties of peas, the so-called "half-dwarfs" can be separated into at least two genetic types. One of these is illustrated by the examples of half-dwarf already mentioned—Velocity, First of All, and Express. These have long internodes, similar to the 40–60 and 20–40 long internode talls, but fewer in number, ranging between 10–20. The other type of half-dwarf has short internodes, similar to the short internodes of the true dwarfs. This type is illustrated by the variety Dwarf Gray Sugar, with internodes ranging in number from 20 to 40. The variety Autocrat, as studied by Keeble and Pellew ('10), probably also belongs in this category.

Half-dwarfs with long internodes crossed with short internode half-dwarfs give long internode talls in F_1 and long internode talls, long internode half-dwarfs, short internode half-dwarfs, and true dwarfs, approximating a 9 : 3 : 3 : 1 ratio in F_2. Similar results from such a cross, so far as the writer can judge, have been obtained by Keeble and Pellew ('10), although they have given them a somewhat different interpretation (see also Lock, '05). Half-dwarfs of each type crossed with similar half-dwarfs, as expected, breed true in F_1, F_2 and later generations. Half-dwarfs of the short internode type crossed with the 20–40 long internode tall type give in F_1 talls with long internodes, which in F_2 produce a population approximating 3 talls with long internodes : 1 half-dwarf with short internodes. The difference in height between such talls and such half-dwarfs is due largely to internode length, the number of internodes in each type being approximately the same. Half-dwarfs with long internodes crossed with talls with long internodes (20–40 type) give talls in F_1 and populations approximating 3 talls : 1 half-dwarf in F_2, both, of course, with long internodes, the difference between them in this case being due to internode number.

True dwarfs (6 inches to 3.5 feet high) in peas all have short internodes, ranging f om 8 to 20 in number. Laxtonian, Nott's Excelsior, and several French varieties obtained through the courtesy of Phillipe Vilmorin are excellent examples. When crossed with the various types of talls, the F_1 generation always consists of talls with long internodes, although large number of internodes may not be completely dominant over small number of internodes in certain cases, e. g., Pois nain à châssis, très hâtif crossed with Wachs Schwert (40–60 internodes tall). In such crosses, the F_1 generation is to be regarded as intermediate, so far as the gross character height is concerned, although this intermediate condition is brought about through incomplete dominance of high over low internode number. Tschermak ('01) also mentions obtaining intermediates in F_1, as regards height, from crosses of talls and dwarfs, though he says nothing about internode

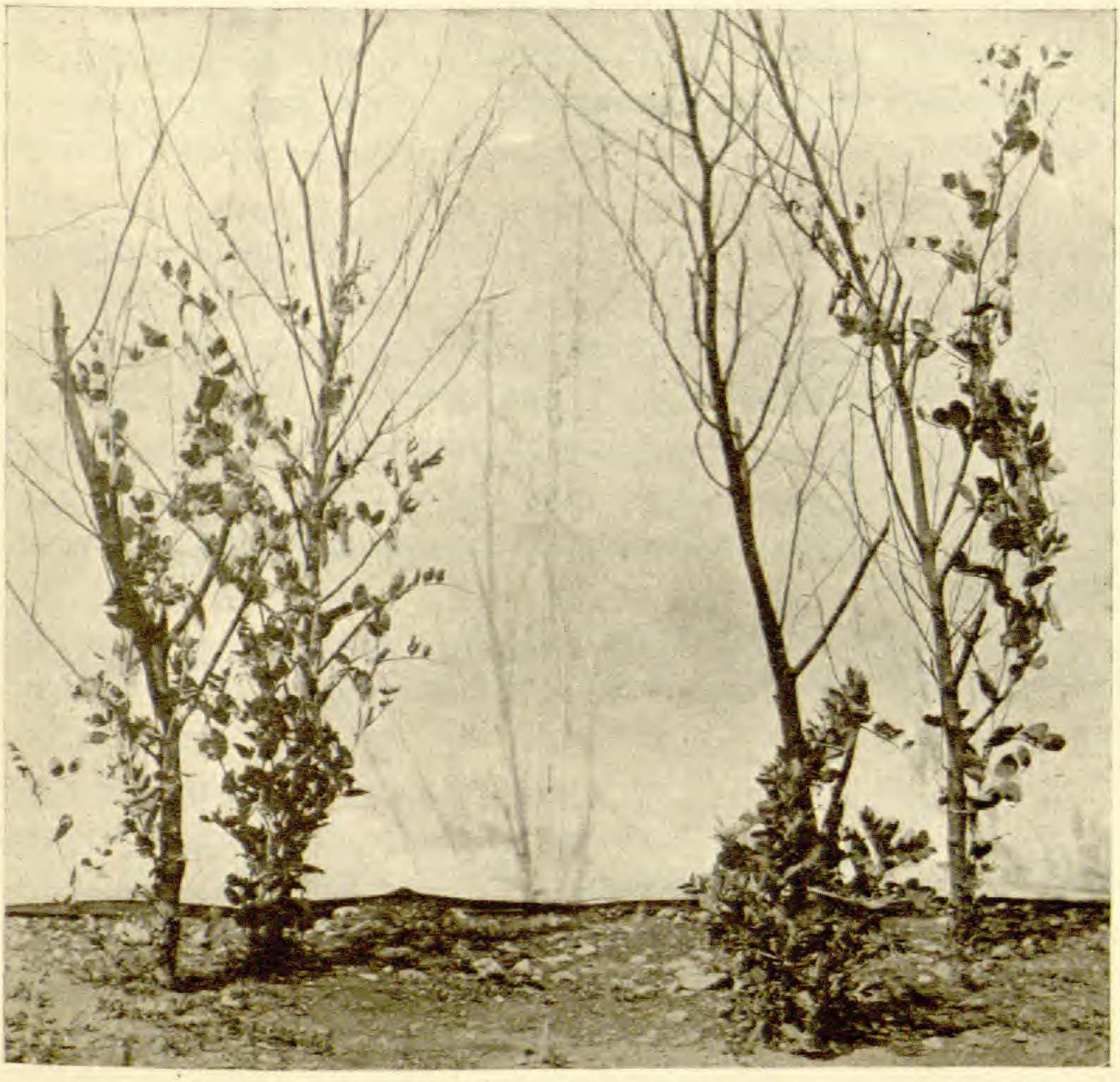

FIG. 1. F_2 generation tall and dwarf segregates from cross of tall × dwarf. Photo from cultures of E. M. East.

number or length. The F_2 generation from tall × dwarf or its reciprocal consists of four classes—talls with long internodes, half-dwarfs with either long or short internodes, and true dwarfs. These approximate a 9 : 3 : 3 : 1 ratio as in the case of short internode half-dwarf × long internode half-dwarf. Laxton ('06) obtained practically these same results. This is the cross usually made to illustrate the inheritance of height and probably the one made by Mendel for the same object. What is usually meant by geneticists, so far as the writer can learn, when discussing inheritance of height in peas, is really the inheritance of difference in internode length. Hence all short internode varieties or segregates, irrespective of actual height or number of internodes, are classed as dwarfs, while all long internode varieties or segregates, irrespective of number of internodes, are classed as talls. Classified in such a manner, the F_2 population from such a cross as described above would have approximately 3 tall (long internodes) : 1 dwarf (all short internodes). The long internode half-dwarfs would be called talls, while the half-dwarfs with short internodes would be called dwarfs (see Bateson *et al.*, '05; Lock, '05, '08; Laxton, '06).

Crosses between half-dwarfs with long internodes and true dwarfs gave half-dwarfs in F_1 and approximately 3 half-dwarf (long internodes) : 1 dwarf (short internodes) in F_2 in the writer's experiments. Bateson ('05) commonly obtained intermediates in F_1 from crosses between half-dwarfs (presumably short internodes) and dwarfs.

The simplest interpretation of the above data involves the presence and absence of at least five genetic factors for height, two of which primarily determine the differences in internode length and three of which are largely responsible for the hereditary differences in number of internodes. These with their expression may be represented as follows:

Le = long internodes
Le_1 = very long internodes
T = 20–40 internodes
T_1 = 40–60 internodes
T_2 = 20–30 internodes

Absences

le = short internodes
t = 10–20 internodes

Le and T have been referred to in previous numbers of this series (White, '17 a and b), Le being the factor isolated by Mendel and confirmed by many later workers. T is referred to by Keeble and Pellew ('10) as the factor for robust stems, but in the writer's interpretation of their results, it determines the difference in internode number.

On the above interpretation, the factorial composition of the three classes of talls would be:

(1) LeT = 20–40 long internodes.
(2) LeT$_1$ = 40–60 long internodes.
(3) Le$_1$T$_2$ = 20–30 very long internodes.

The factorial composition of the half-dwarfs would be:

(4) Let = 10–20 long internodes.
(5) leT = 20–40 short internodes.

The true dwarfs on this scheme would represent the absences of Le and T or (6) let.

Sufficient data have not yet been accumulated to determine in any detail the relations of these factors to each other except in the case of Le and T. Varieties with formula (1) crossed with (4) should and do give all long internode talls in F$_1$ and talls and half-dwarfs (long internode) in F$_2$. Combination (1) × (5) gives long internode talls in F$_1$ and approximately 3 talls (long internodes) : 1 half-dwarf (short internodes) in F$_2$. Combination (1) × (6) gives all long internode talls in F$_1$ and an F$_2$ population approximating 9 tall (l.i.) : 3 hd. (l.i.) : 3 hd. (s.i.) : 1 dwarf (s.i.). The two half-dwarf types, (4), (5) crossed with each other give all long internode talls in F$_1$, but an F$_2$ population similar to (1) × (6). Half-dwarf varieties (5) × dwarfs give intermediates in F$_1$ in some cases. The writer has no data on this cross as yet. Half-dwarf varieties with the formula Let (4) crossed with dwarfs (6) give all long internode half-dwarfs in F$_1$, and approximately 3 half-dwarfs : 1 dwarf in F$_2$.

Critics of Mendelian methods and conceptions will say again, as the above results are noted, "another unit-character has been split up." But the writer wishes to emphasize that with the same genetic pea material that Mendel and others have used to obtain the F$_2$ ratio of 3 talls : 1 dwarf, the same results will still be secured. The difference in interpretation has come from more detailed studies and the inheritance of height in peas has become complex only because of studies on new or distinctly different material, the characters of which, there is reason to believe, are due to distinct mutations.

A large series of crosses involving height is in progress, and the data from these will be published in detail.

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